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Two new species of zooplanktivorous haplochromine cichlids from Lake Victoria, Tanzania

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Abstract

Two new species of zooplanktivorous haplochromine cichlids from Lake Victoria, Tanzania, are described and illustrated. These species closely resemble each other. Their affinities to other zooplanktivorous haplochromines from Lake Victoria are discussed. *Haplochromis argens* **sp. n.**, which featured under nicknames (mainly *H.* "argens") in more than 50 papers, was caught both in the Mwanza Gulf and the Emin Pasha Gulf, whereas *H. goldschmidti* **sp. n.** was only found in the Emin Pasha Gulf. Of the latter species only males are available, but it seems unlikely that it represents a case of male colour polymorphism as several presumably unrelated characters differ in sympatry between the two species, suggesting that there is no gene flow. Statistical analysis revealed that the overall difference between the two species is greater than that between the populations from the two locations. Body depth of the two species in sympatry in the Emin Pasha Gulf was more similar than that of *H. goldschmidti* **sp. n.** and the allopatric population of *H. argens* **sp. n.** from the Mwanza Gulf, which may indicate an overall environmental effect. However, several measurements related to the width of snout and mouth differed more between the populations of the two species in sympatry than between the allopatric populations. In contrast to a group of zooplanktivorous species that recovered successfully after environmental changes in the lake, *H. argens* **sp. n.** is among a group that became extremely rare and probably is in danger of extinction; the conservation status of *H. goldschmidti* **sp. n.** is currently unknown.

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Keywords
Allopatric populations, Cichlidae, colour polymorphism, East Africa, endangered species, *Haplochromis*, zooplanktivores

Introduction

In this paper two zooplanktivorous haplochromine species from Lake Victoria are described. One of these species, nicknamed *Haplochromis* "argens," was common in the Mwanza Gulf until 1985 and also caught in other areas in the Tanzanian part of the lake. Since the late 1970s, this species has been the subject of studies on ecology (e.g. Witte 1984b, Goldschmidt et al. 1990), morphology (e.g. van der Meer and Bowmaker 1995, van der Meer et al. 1995), behavioral biology (Smith and Wooton 1994) and physiology (Rosenberger and Chapman 2000, Melnychuk and Chapman 2002). The second species, which closely resembles *H.* "argens," was nicknamed *H.* "dusky argens". It was only caught in the Emin Pasha Gulf in 1985 and 1986, concomitantly with *H.* "argens" (Goldschmidt and de Visser 1990).

Up to the 1980s, the zooplanktivorous haplochromines were, both in number and biomass, the second most abundant group of demersal fishes in sub-littoral areas of the Mwanza Gulf. A one hour tow of a bottom otter trawl (head rope 25 m) contained on average 1140 kg of haplochromines, of which 27% (more than 100,000 individuals) were zooplanktivores (Goldschmidt et al. 1993, Witte et al. 2012b). During the 1980s it became clear that the ecosystem of Lake Victoria was subject to a perturbation of an enormous magnitude. The population of Nile perch, *Lates niloticus* (Linnaeus 1758), an introduced predator, boomed (Ogutu-Ohwayo 1990, Goudswaard et al. 2008) and concomitantly widespread eutrophication became apparent (e.g. Kaufman 1992; Witte et al. 1992a; Hecky 1993; Hecky et al. 1994, 2010; Seehausen et al. 1997a; Wanink et al. 2001). As a result, the haplochromine cichlids in the sub-littoral waters of Lake Victoria almost vanished (Ogutu-Ohwayo 1990; Witte et al. 1992b).

From 1987 to 1992, haplochromines were extremely rare in trawl catches in the Mwanza Gulf; however, with the subsequent decline of Nile perch due to heavy fishing, a slow recovery of some zooplanktivorous species was noticed (Seehausen et al. 1997b; Witte et al. 2000, 2007a, b). This resurgence is continuing till the present day. In 2005 the zooplanktivorous haplochromines, which used to be second in importance after the detritivorous haplochromines, were the dominant trophic group and even more abundant than before the environmental changes (Witte et al. 2007a). Initially, *H.* "argens" was not present among the resurgent zooplanktivores, but the species has been caught again since 2002, albeit in very low numbers (Wanink JH, Kishe-Machumu M and Witte F, unpublished data).

As *H.* "argens" has already made its appearance in more than 50 articles, is bred in captivity by scientists and hobbyists, and currently is caught again in the lake, a formal taxonomic description is urgently needed and presented in this paper.

In the Emin Pasha Gulf, males of *H.* "argens" and males that resembled this species were caught in the same hauls. The latter males differed from *H.* "argens" in aspects of their overall nuptial body colouration, the colour of their caudal fin, and number and position of the egg spots on the anal fin (Goldschmidt and de Visser 1990). These males were referred to as *H.* "dusky argens" by Goldschmidt and de Visser (1990). The taxonomic status of these specimens is investigated, and they are described as a new species in this paper.

Material and methods

The type specimens of both species were collected in the Tanzanian part of Lake Victoria. All type material was collected between May 1975 and August 1986, before the collapse of the haplochromines in the Tanzanian part of the lake due to the Nile perch upsurge and eutrophication (e.g. Witte et al. 1992a, b, 2012a; Seehausen et al. 1997a; Wanink et al. 2001; Goudswaard et al. 2008). *Haplochromis* "argens" was collected in the Mwanza Gulf (between Nyamatala Island and Hippo Island, depth range about 6–16 m) and in the Emin Pasha Gulf (Fig. 1), mainly with bottom trawls, occasionally with gill nets. The type material of *H.* "argens" comprises 77 specimens (size range of 53.1–77.4 mm SL): 36 males and eight females from the Mwanza Gulf and 33 males and no females from the Emin Pasha Gulf. The type specimens (51 males; size range 50.7–69.2 mm SL) of *H.* "dusky argens" were collected in the Emin Pasa Gulf with bottom trawls on 22 and 23 July 1985, at two localities (depth range 4–8 m; Fig. 1). The live colours of some individuals were photographed in a small perspex tank filled with water (Barel et al. 1977). Immediately after they were caught, the fish were stored on ice. In the laboratory they were preserved in 10% formalin neutralized with borax. After several months to several years the fishes were sent to the Netherlands, where they were rinsed with tap water and stepwise transferred to 70% ethanol.

Ten male specimens of *H.* "argens" were dissected. The oral jaws were removed from nine specimens and the pharyngeal jaws from four specimens. From six specimens the first gill arch was dissected. Of *H.* "dusky argens," six specimens were dissected. From five specimens the oral jaws and the intestines were removed and from three specimens the pharyngeal jaws and the first gill arch. The description of the shape of the oral and pharyngeal jaws and their dentition was based on the dissected elements, as were the counts of the gill filaments.

Linear measurements and counts were collected from 57 specimens of *H.* "argens" and 19 specimens of *H.* "dusky argens." Counts included numbers of scales, teeth, gill rakers and vertebrae, the latter obtained from radiographs. Additional specimens for which counts and measurements were not made are also designated as type specimens; these include specimens used for colour descriptions (from colour slides) and other qualitative characters, specimens used for dissection, and specimens from which tissue samples for DNA analysis had been taken. Terminology and measurements follow

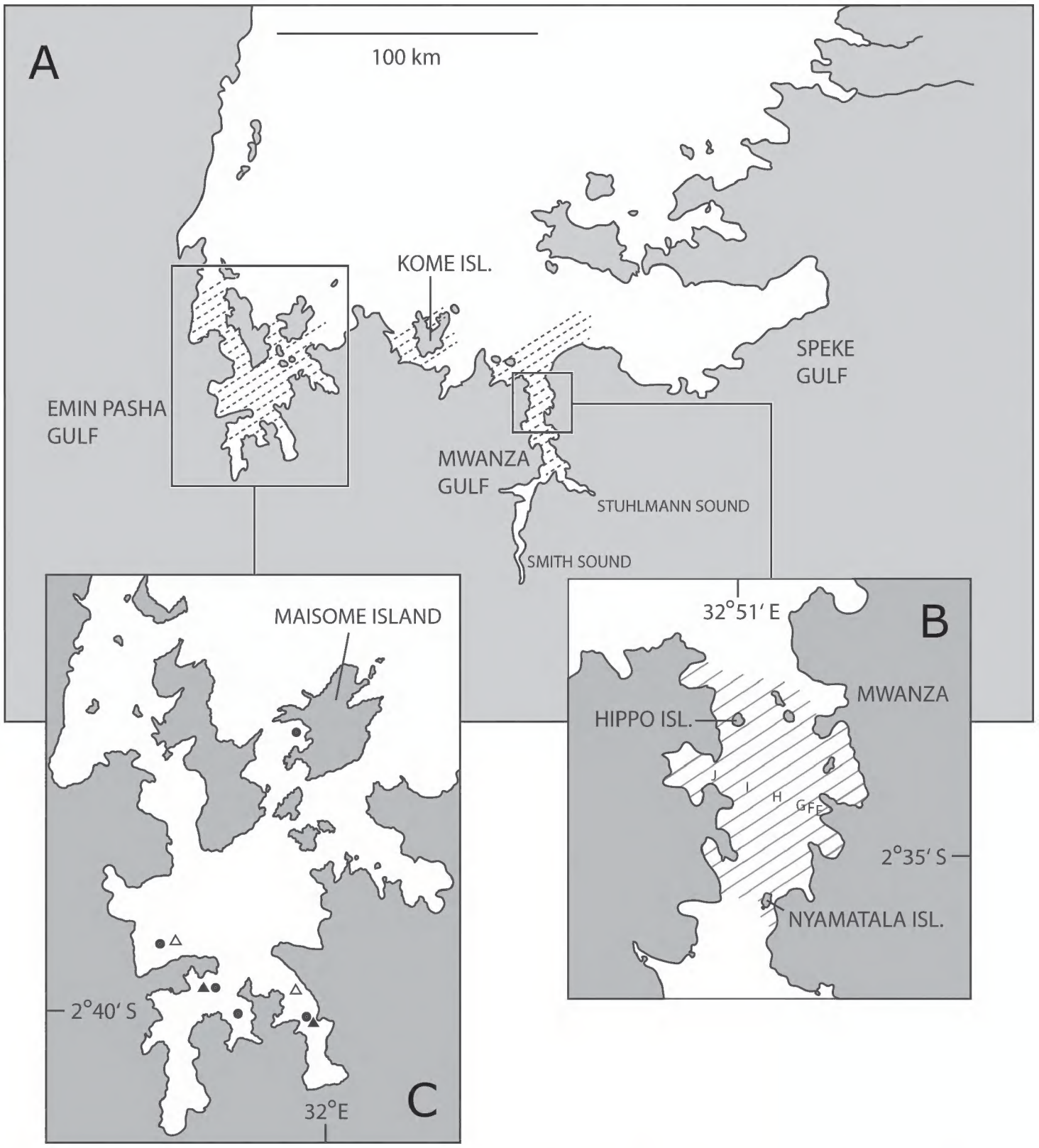

Figure 1. Tanzanian part of Lake Victoria. **A**, distribution of *Haplochromis argens* sp. n. (hatched area) **B** Mwanza Gulf with catch localities of type specimens of *H. argens* sp. n. (hatched area); E to J represent stations along the research transect where data on abundance of *H. argens* sp. n. were collected **C** Emin Pasha Gulf with catch localities of type specimens of *H. argens* sp. n. (filled circles) and type specimens of *H. goldschmidti* sp. n. (filled triangles); open triangles indicate other catch localities of *H. goldschmidti* sp. n.

Barel et al. (1977), Hoogerhoud and Witte (1981) and Witte and Witte-Maas (1981). Abbreviations used in the text are explained in Table 1.

Measurements were taken to the nearest 0.1 mm using digital callipers with needles glued to the ends. For comparison with earlier described haplochromine species from Lake Victoria (e.g. Greenwood 1981) we transformed the measurements to proportions (percentages) of standard length (SL) or head length (HL). We present the

Table 1. Measurements of *Haplochromis argens*, proportional to standard length or head length. Means and standard deviations were calculated over all measured type specimens, including the holotype.

		Holotype	Paratypes (n = 56)	Mean ± SD (n = 57)
standard length SL (mm)		67.3	53.1–75.5	63.1 ± 5.4
body depth (BD)	%SL	28.8	26.0–30.7	28.2 ± 1.1
pectoral fin length (PFL)	%SL	27.3	25.4–30.9	27.8 ± 1.2
caudal peduncle length (CPL)	%SL	21.7	18.5–23.5	20.7 ± 1.1
caudal peduncle depth (CPD)	%SL	9.7	9.1–11.1	10.0 ± 0.5
caudal fin length (CFL)	%SL	22.7	20.1–25.5	23.9 ± 1.0
head length (HL)	%SL	31.7	31.0–35.6	32.9 ± 0.9
snout length (SnL)	%HL	26.3	23.6–29.7	26.6 ± 1.6
snout width (SnW)	%HL	27.6	20.6–27.8	24.5 ± 1.7
head width (HW)	%HL	41.3	32.0–43.8	40.0 ± 1.8
interorbital width (IOW)	%HL	22.1	18.8–23.8	20.8 ± 1.1
preorbital width (POW)	%HL	24.4	20.6–25.7	23.4 ± 1.2
lachrymal width (LaW)	%HL	21.6	17.3–23.2	20.2 ± 1.4
preorbital depth (POD)	%HL	15.5	13.1–18.7	15.3 ± 1.2
eye length (EyL)	%HL	36.6	30.9–39.0	35.7 ± 2.1
eye depth (EyD)	%HL	33.4	27.4–35.2	31.6 ± 1.7
cheek depth (ChD)	%HL	16.9	11.9–20.5	16.7 ± 1.7
lower jaw length (LJL)	%HL	40.4	37.6–44.3	40.5 ± 1.5
lower jaw width (LJW)	%HL	13.6	11.0–15.6	13.2 ± 1.0
EyD/EyL		0.9	0.8–1.0	0.9 ± 0.04
LJL/LJW		3.0	2.6–3.8	3.1 ± 0.27

proportional measurements to the nearest 0.1%, but it should be noted that they may deviate ± 0.2% because measurements were only accurate to the nearest 0.1 mm; the same is true for measurements presented in other species descriptions of Lake Victoria haplochromines. Unless stated otherwise, qualitative characters described as being relatively small or large refer to size relative to that of *Haplochromis* (*Astatotilapia*) *elegans* Trewavas, 1933. Morphologically, this insectivore from Lake George is a modal haplochromine cichlid. Its skeletal elements are described in Barel et al. (1976).

A comparison was made between *H.* "dusky argens" and the two populations of *H.* "argens" from the Mwanza Gulf and the Emin Pasha Gulf. As no females are available for *H.* "dusky argens," we only compared males. To test for differences in linear measurements of the three populations in general, MANCOVA was used. ANCOVAs were used to identify differences among the three populations in specific linear measurements. Data were log-*e* transformed to achieve linearity. The factors "Species" (two species) and "Location" (two locations) were investigated, and log standard length (SL) was used as covariate. Parameter estimates derived from the GLM (analysis of covariance) procedure were used to define and plot the power function between SL and individual taxonomic measurements and to calculate the relative differences in individual measurements between *H.* "dusky argens" and the two populations of *H.* "argens". For testing of interactions and main effects, Sum of Squares Type II was

used. Whether the residuals followed a normal distribution was investigated with the Kolmogorov-Smirnov Test. For statistical analysis of the morphometric data, SPSS version 14.0 for Windows was used.

Live (juvenile) *H. (Psammochromis) cassius* Greenwood & Barel, 1978, are similar to *H.* "argens". To compare *H.* "argens" with *H. cassius* which was described from only five females (some of them much larger than *H.* "argens"), we used measurements from six specimens of *H. cassius*: three specimens from the collection of Naturalis Biodiversity Center (RMNH.PISC.63199, RMNH.PISC.63200 and RMNH.PISC.74187) and three specimens from the collection of the Natural History Museum, London (BMNH 1987.2.4.1, BMNH 1987.2.4.2 and BMNH 1987.2.4.5). These specimens have a size range (67.4 – 79.3 mm SL) comparable to that of *H.* "argens".

To describe changes in abundance of *H.* "argens" during the period 1979 to 2011, we compared the frequency of occurrence (= percentage of catches containing one or more individuals of *H.* "argens") and the average numbers of individuals that were caught in trawl tows of 10 minutes duration with a small boat (20 or 25 hp) on a research transect in the Mwanza Gulf (Fig. 1; Witte et al. 1992). A bottom otter trawl (head rope 4.6 m, codend mesh 5 or 15 mm) was used during the day and a surface trawl (beam 4.5 m, codend mesh 5 mm) during the night.

Specimens referred to in this study are deposited in the Naturalis Biodiversity Center, Leiden (RMNH), the American Museum of Natural History, New York (AMNH), the Natural History Museum, London (BMNH) and the National Museum of Nature and Science, Tsukuba (NSMT), Japan.

Results

Species descriptions

***Haplochromis argens* de Zeeuw, Westbroek & Witte, sp. n.**
urn:lsid:zoobank.org:act:B0288AFB-9C11-4D81-9B7B-E551951A7B2D
http://species-id.net/wiki/Haplochromis_argens
Figs 2–5, Tables 1,2

Cheironyms used. Haplochromis argens: Goldschmidt 1994: 179, 199–200; *Haplochromis argens*; Verheyen et al. 1989: 93, 94, 96; van der Meer 1995: 26, 30–32; van der Meer and Bowmaker 1995: 232–239; Goldschmidt 1996: 164, 184–185; Hilder and Pankhurst 2003: 194; Collin et al. 2004: 769; Carleton et al. 2008.

Haplochromis "argens"; Zihler 1982: 568; Barel 1983: 384, 385, 407, 418; Witte 1984a: 604, 611; Witte 1984b: 159–161, 163; Barel 1985: chapter 1, 384, 385, 407, 418; Gottfried 1986: 1029; Witte 1987, chapter 1: 611, chapter 2: 67, 76, chapter 3: 8–13, 19; Goldschmidt 1989a: 24, 27, 29–39, 41, 42, 44, 45, 53, 55, 58, 59, 61–63, 65–69, 71–75, 77, 82, 84, 86–89, 97–101, 103, 118, 119, 148, 158, 160, 162, 166; Goldschmidt 1989b: 122–126, 129–131; Wanink et al. 1989: 25; van der Meer 1989:

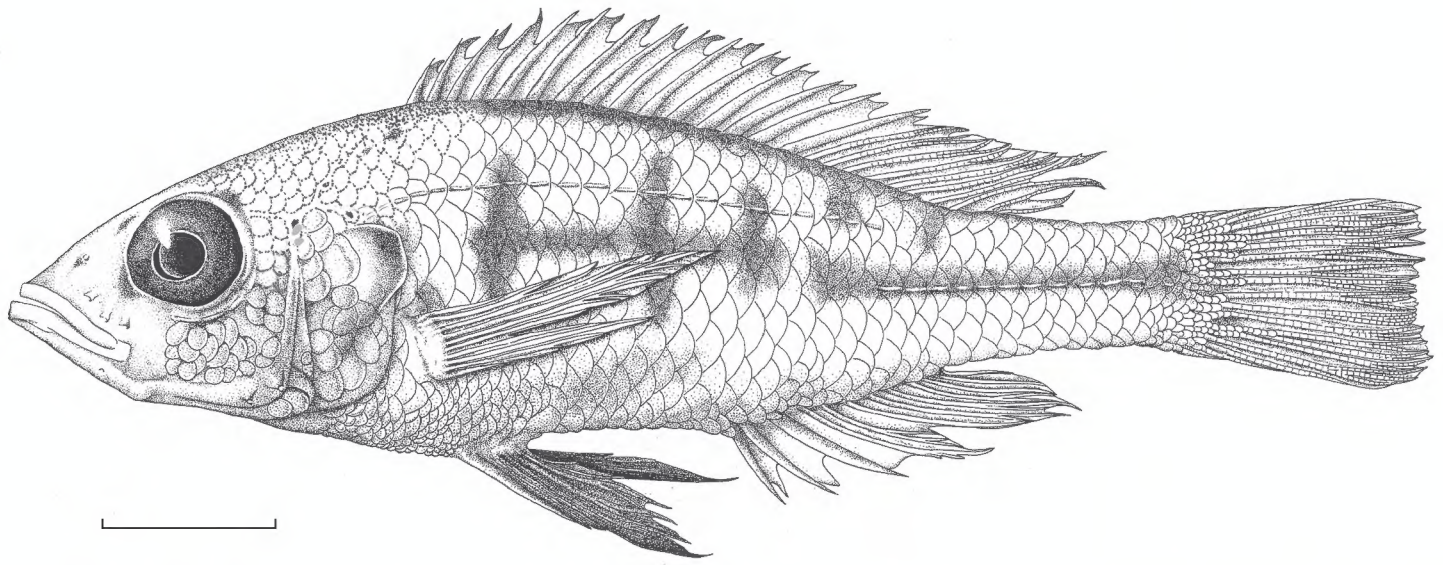

Figure 2. Habitus of *Haplochromis argens* sp. n. ♂ (holotype, RMNH.PISC.83588). Scale bar equals 10 mm. Drawing by I. Westbroek, missing (= dotted) scales added by M. van Oijen.

52, 53; Goldschmidt and de Visser 1990: 129, 130, 132; Goldschmidt et al. 1990: 344, 346–351, 353; Goldschmidt and Witte 1990: 356–367; Barel et al. 1991: 262; Goldschmidt 1991: 181, 182, 185, 187; van der Meer 1991a: 91–94, 96; van der Meer 1991b: 3, 5, 6, 9–12, 14–22, 24–26, 28, 68, 76, 77, 83, 85–87, 89–93, 99, 101, 104; Goldschmidt and Witte 1992: 104; Kaufman 1992: 848, 849; Witte et al. 1992b: 11, 13, 17, 25, 27, 28; Barel 1993: 366; Smith and Wootton 1994: 99–103; Balshine-Earn 1995: 5; Seehausen 1995: 143, 146; Seehausen and Witte 1995: 101; van der Meer et al. 1995: 116–129; Smith and Wootton 1995: 12; Anker and Dullemeijer 1996: 4–11; de Visser and Barel 1996: 4; Seehausen 1996: 51, 55, 255, 256; Smit and Anker 1997: 9–17; Seehausen et al. 1997b: 899; Witte et al. 1997: 591; Wanink 1998: 159, 232; Rinkes 1999: 46, 47, 54, 56–58, 60, 62, 76, 77, 79, 97; de Visser 2000: 18; Tacon et al. 2000: 63; Witte and Wanink 2000: 78–81, 84; Seehausen et al. 2003: 272; Witte et al. 2005: 320; Kishe-Machumu 2012: 35; van Rijssel and Witte 2012.

H. "Argens"; Kaufman and Seehausen 1995: 148.

Haplochromis (?) "argens"; Wanink and Witte 2000: 563; Witte et al. 2000: 234, 235, 237; Witte et al. 2003: 108; Niemantsverdriet 2005: 151, 155; Witte et al. 2007a: 1153.

Haplochromis sp. "argens"; Mizoiri et al. 2008: 228, 241, 254.

Yssichromis argens; van Staaden et al. 1995: 168; Chapman et al. 1995: 1277, 1279–1282, 1285; Huber et al. 1997: 170; Rosenberger and Chapman 2000: 498; Melnychuk and Chapman 2002: 107.

Yssichromis sp. "argens"; Mizoiri et al. 2008: 228.

Type-locality. Tanzania, Lake Victoria, Mwanza Gulf (ca 2°29'–2°36'S; 32°48'–32°54'E) and Emin Pasha Gulf (ca 2°18'–2°41'S; 31°47'–31°59' E).

Holotype. RMNH.PISC.83588[4], ♂, 67.3 mm SL, Tanzania, Lake Victoria, Mwanza Gulf, 8.iii.1979, HEST.

Paratypes. All type specimens collected by *Haplochromis* Ecology Survey Team (HEST) in Mwanza Gulf, Tanzania, Lake Victoria, except where noted otherwise.

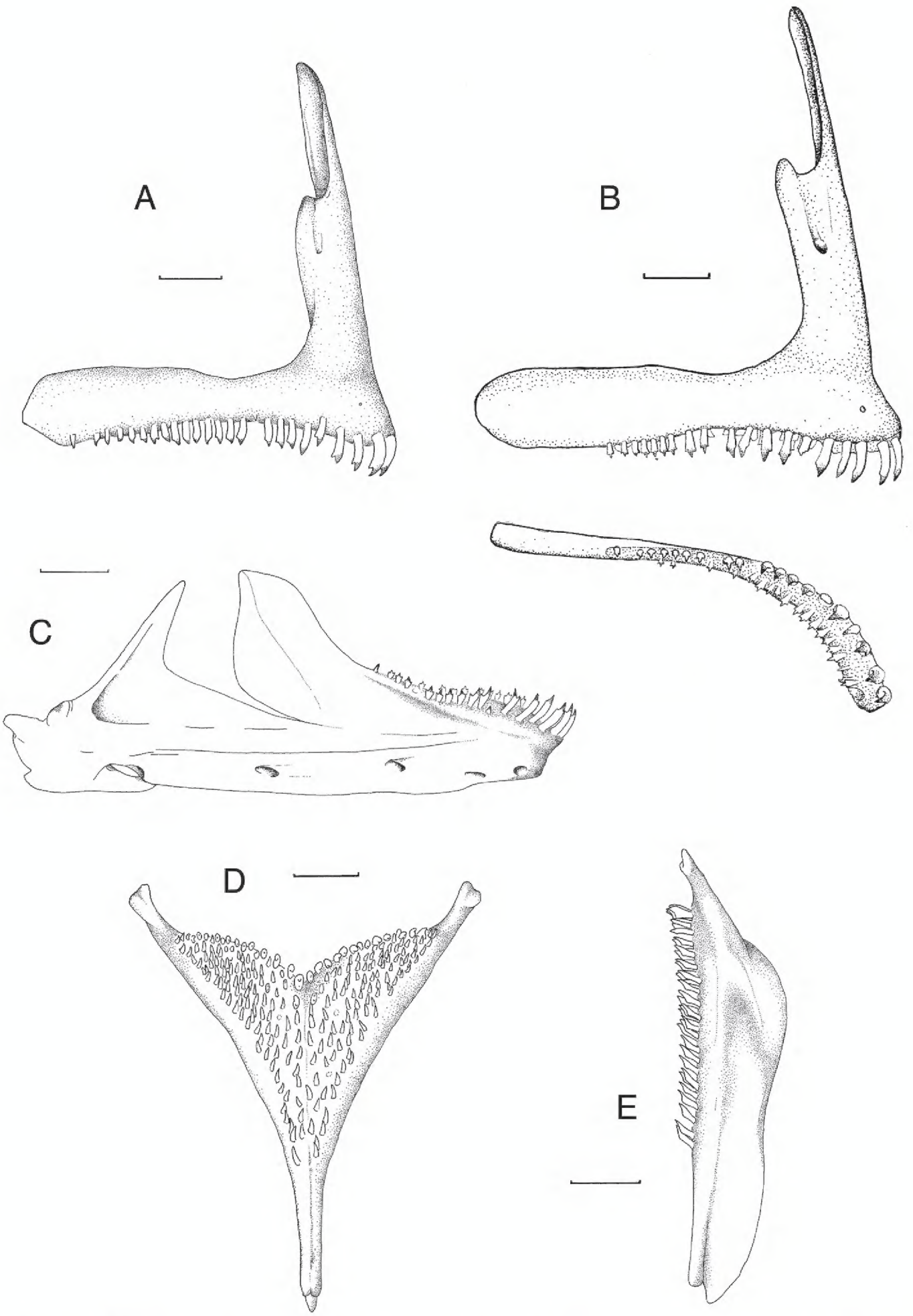

Figure 3. Skeletal elements of *Haplochromis argens* sp. n. **A** Right premaxilla, lateral view (RMNH. PISC.83705) **B** Right premaxilla, lateral (top) and occlusal (bottom) views (RMNH.PISC.83621), illustrating, for this species, a rare case of a posteriorly edentulous premaxilla **C** Right lower jaw, lateral view (RMNH.PISC.83697) **D** Lower pharyngeal element, dorsal view (RMNH.PISC. 83706) **E** Lower pharyngeal element, lateral view (RMNH.PISC.83706). Scale bars equal 1 mm. **A, C, D** drawn by I. Westbroek, **B** by M. van Oijen.

Size of specimens given as standard length. RMNH.PISC.72831[5], ♀, 71.0 mm, 30.v.1980; RMNH.PISC.72884[5, 6], ♂, 74.4 mm, 31.v.1980; RMNH.PISC.73097, ♀, 71.3 mm, 27.ix.1977; RMNH.PISC.81202[5], ♀, 65.6 mm, 11.v.1978; RMNH.PISC.83587, ♂, 77.4 mm, 31.v.1975; RMNH.PISC.83589[4], ♀, 75.5 mm, 21.iv.1980; RMNH.PISC.83590[4], ♂, 68.2 mm, 22.iv.1980; RMNH.PISC.83606[4], ♂, 73.7 mm, 22.iv.1980; RMNH.PISC.83607[4], ♂, 65.7 mm, 15.iv.1980; RMNH.PISC.83608[5], ♂, 65.7 mm, 31.v.1975; RMNH.PISC.83609[4], ♂, 67.4 mm, 22.iv.1980; RMNH.PISC.83610[4], ♂, 66.2 mm, 30.ix.1977; RMNH.PISC.83611[4], ♂, 69.5 mm, 30.ix.1977; RMNH.PISC.83612[4], ♀, 71.1 mm, 30.ix.1977; RMNH.PISC.83613[4], ♀, 68.1 mm, 30.ix.1977; RMNH.PISC.83614[4], ♀, 71.9 mm, 8.ix.1977; RMNH.PISC.83615[4], ♂, 57.7 mm, 8.ix.1977; RMNH.PISC.83616[4], ♂, 70.2 mm, 19.viii.1977; RMNH.PISC.83617[4], ♀, 71.5 mm, 19.viii.1977; RMNH.PISC.83618[4], ♂, 66.1 mm, 7.ix.1977; RMNH.PISC.83619[4], ♂, 66.5 mm, 21.xii.1977; RMNH.PISC.83620[4], ♂, 65.8 mm, 10.x.1977; RMNH.PISC.83621[1], ♂, circa 70 mm, 30.ix.1977; RMNH.PISC.83622[5], ♂, 59.3 mm, 22.vi.1985, Emin Pasha Gulf; RMNH.PISC.83623[5], ♂, 57.2 mm, 22.vi.1985, Emin Pasha Gulf; RMNH.PISC.83624[5], ♂, 59.6 mm, 23.vi.1985, Emin Pasha Gulf; RMNH.PISC.83625[4], ♂, 58.3 mm, 23.vi.1985, Emin Pasha Gulf; RMNH.PISC.83626[4], ♂, 58.5 mm, 23.vi.1985, Emin Pasha Gulf; RMNH.PISC.83627[4], ♂, 54.3 mm, 23.vi.1985, Emin Pasha Gulf; RMNH.PISC.83628[4], ♂, 59.6 mm, 23.vi.1985, Emin Pasha Gulf; RMNH.PISC.83629[4], ♂, 55.4 mm, 23.vi.1985, Emin Pasha Gulf; RMNH.PISC.83630[4], ♂, 53.1 mm, 23.vi.1985, Emin Pasha Gulf; RMNH.PISC.83631[4], ♂, 66.8 mm, 23.vi.1985, Emin Pasha Gulf; RMNH.PISC.83632[4], ♂, 67.0 mm, 23.vi.1985, Emin Pasha Gulf; RMNH.PISC.83633[4], ♂, 60.4 mm, 23.vi.1985, Emin Pasha Gulf; RMNH.PISC.83634[4], ♂, 53.9 mm, 23.vi.1985, Emin Pasha Gulf; RMNH.PISC.83635[4], ♂, 62.6 mm, 23.vi.1985, Emin Pasha Gulf; RMNH.PISC.83636[4], ♂, 66.6 mm, 23.vi.1985, Emin Pasha Gulf; RMNH.PISC.83637[4], ♂, 69.2 mm, 23.vi.1985, Emin Pasha Gulf; RMNH.PISC.83638[4], ♂, 65.8 mm, 23.vi.1985, Emin Pasha Gulf; RMNH.PISC.83639[4], ♂, 61.3 mm, 23.vi.1985, Emin Pasha Gulf; RMNH.PISC.83640[4], ♂, 73.4 mm, 23.vi.1985, Emin Pasha Gulf; RMNH.PISC.83641[4], ♂, 64.1 mm, 23.vi.1985, Emin Pasha Gulf; RMNH.PISC.83642[4], ♂, 63.1 mm, 23.vi.1985, Emin Pasha Gulf; RMNH.PISC.83643[4], ♂, 63.7 mm, 23.vi.1985, Emin Pasha Gulf; RMNH.PISC.83644[4], ♂, 62.1 mm, 23.vi.1985, Emin Pasha Gulf; RMNH.PISC.83645[4], ♂, 64.1 mm, 23.vi.1985, Emin Pasha Gulf; RMNH.PISC.83646[4], ♂, 61.6 mm, 23.vi.1985, Emin Pasha Gulf; RMNH.PISC.83647[4], ♂, 59.8 mm, 25.viii.1981; RMNH.PISC.83648[4], ♂, 61.6 mm, 10.x.1977; RMNH.PISC.83649[4], ♂, 61.5 mm, 21.xii.1977; RMNH.PISC.83650[4], ♂, 57.7 mm, 6.iii.1979; RMNH.PISC.83651[4], ♂, 60.6 mm, 13.vii.1979; RMNH.PISC.83652[4], ♂, 58.0 mm, 1.ii.1979; RMNH.PISC.83653[4], ♂, 53.5 mm, 18.xi.1981; RMNH.PISC.83655[4], ♂, 61.8 mm, 14.v.1979; RMNH.PISC.83656[4], ♂, 59.0 mm, 27.iii.1979; RMNH.PISC.83657[4], ♂, 61.6 mm, 27.iii.1979; RMNH.PISC.83660[4], ♂, 56.8 mm, 12.iii.1979; RMNH.PISC.83661[4], ♂, 57.9 mm, 12.iii.1979; RMNH.PISC.83662[4], ♂, 59.7 mm, 14.v.1979; RMNH.PISC.83663[4], ♂, 58.6 mm, 14.v.1979; RMNH.PISC.83673[4], ♂, 55.5 mm, 23.vi.1985, Emin Pasha Gulf; RMNH.PISC.83688[1–3],

Figure 4. Live colours of *Haplochromis argens* sp. n. **A** sexually active ♂, 59.3 mm SL (paratype, RMNH.PISC.83622), Emin Pasha Gulf **B** sexually active ♂, 72.1 mm SL (paratype, RMNH. PISC.84067), Mwanza Gulf.

♂, 61.4 mm, 6.iii.1979; RMNH.PISC.83689[1–3], ♂, 62.2 mm, 14.v.1979; RMNH. PISC.83694[1, 5], ♂, 63.1 mm, 21.vi.1985, Emin Pasha Gulf; RMNH.PISC.83697[1, 5], ♂, 59.1 mm, 23.vi.1985, Emin Pasha Gulf; RMNH.PISC.83698[1–3, 5], ♂, 61.0 mm, 23.vi.1985, Emin Pasha Gulf; RMNH.PISC.83703[3, 6], ♂, 66.4 mm, 23.vi.1985, Emin Pasha Gulf; RMNH.PISC.83704[1, 3, 6], ♂, 68.4 mm, 23.vi.1985, Emin Pasha Gulf; RMNH.PISC.83705[1–3, 6], ♂, 67.5 mm, 23.vi.1985, Emin Pasha Gulf; RMNH. PISC.83706[1, 5], ♂, 68.8 mm, 27.vi.1985, Emin Pasha Gulf; RMNH.PISC.84067[5, 7], ♂, 72.1 mm, 15.viii.1986; AMNH 255035[4], ♂, 62.2 mm, 14.v.1979; BMNH 2012.1.5.2 [4], ♂, 62.8 mm, 3.v.1979; NSMT-P 106959[4], ♂, 62.6 mm, 3.v.1979.

[1] dissected to describe oral jaws; [2] dissected to describe pharyngeal jaws; [3] dissected to count gill filaments; [4] proportional measurements taken (Table 1); [5]colour picture available; [6]colour picture of anal fin available; [7] specimen of which Dr E. Verheijen, Royal Belgian Institute of Natural Sciences, has taken a tissue sample for DNA analysis.

Diagnosis. Small sized (< 8 cm SL), slender (BD < 31% SL), micrognathic (LJL < 45% HL) zooplanktivorous *Haplochromis* species with slightly curved to straight dorsal head profile. Relatively long and slender, mainly bicuspid, teeth in oral jaws. Premaxillary dentigerous area extending almost to caudal end of dentigerous arm. Both

males and females silvery with conspicuously ivory-white lips. Three to five, generally faint vertical stripes on flank; faint traces of a dark mid-lateral band occasionally present. Males with yellow to greenish sheen on flank.

Description. Proportional measurements of type material given in Table 1.

Habitus. See Fig. 2. Body slender. Dorsal head profile straight to slightly curved, occasionally moderately curved. Premaxillary pedicel slightly prominent. Mouth oblique. Lips not thickened. Medial part of premaxilla slightly expanded. Caudal part of maxilla not bullate. Vertical through caudal tip of maxilla running through iris, just rostral to pupil. Lateral snout outline isognathous and obtuse, in larger specimens slightly prognathous. Jaws equal anteriorly or lower jaw slightly protruding. Mental prominence slightly pronounced. Retro-articular processes of right and left mandible touching each other, interrupting ventral body outline. Eye approximately circular and medium to large. Generally an aphakic aperture present in pupil. Cephalic lateral line pores not enlarged.

Scales. Cheek, gill cover and rostral part of dorsal head surface covered with cycloid scales. Nape and rostral part of dorsum with mixture of cycloid and weakly ctenoid scales. Chest with ctenoid, weakly ctenoid and some cycloid scales. Scales on remaining part of body mainly ctenoid. Scales on chest smaller than those on ventral and ventro-lateral part of body; size transition gradual. Small elongated scales on basal quarter to half of caudal fin. Three to seven (mode 6) scales between upper lateral line and dorsal-fin origin, four to eight (mode 6) between pectoral- and pelvic-fin bases.

Fins. Pelvic fins just reaching or slightly surpassing rostral-most point of anal-fin origin. Pelvic fins with first soft rays slightly produced in both sexes, in males occasionally filamentous. Caudal tip of anal fin not reaching caudal-fin origin. Caudal-fin outline truncate to slightly emarginate.

Gill apparatus. Description based on lateral gill rakers and lateral hemibranch of first gill arch. Number of gill rakers on lower part of gill arch 11–12. Lower two to three rakers reduced (= very short), next one to two short, followed by two to six slender and longer ones. Remaining rakers hooked, bifid, trifid or quadrifid. Rakers generally closely set, viz. touching each other over major part of length. Number of gill filaments 94 to 106.

Viscera. Ratio between intestine length and SL: 1.0–1.4 (n = 25).

Oral jaws. (Fig. 3 A–C) Premaxillary ascending arm equal to or longer than dentigerous arm (asc./dent. arm ratio 1.0 to 1.1). Angle between the arms 77° to 81°. Symphyseal articulation facet not present. Lower jaw slightly more elongated than generalized type (length/height ratio 2.3 to 2.5). Upper half of dentary with distinct outwardly directed flare. Mental prominence slightly pronounced.

Oral teeth shape. (Fig. 3 A–C) Generally teeth in outer row of both premaxilla and lower jaw bicuspid or weakly bicuspid, with some unicuspid or tricuspid teeth interspersed. In specimens over 65 mm SL, weakly bicuspids and unicuspids may dominate. Major cusp of bicuspids isoscelene to subequilateral, protracted and acutely pointed. Flange generally absent, when present very small. Minor cusp weakly developed to distinct, relatively short compared to major cusp. Cusp gap wide. In labial view, neck slender to moderately slender, crown not or slightly expanded. In lateral

Figure 5. Preserved colours of *Haplochromis argens* sp. n. ♂ 67.3 mm SL (holotype, RMNH. PISC.83588). Scale bar equals 10 mm.

view, crown compressed. Outer-row teeth in both premaxilla and lower jaw recurved. Inner rows in both jaws with mainly tricuspid or weakly tricuspid teeth.

Oral teeth size. Outer-row teeth relatively long and slender, gradually decreasing in size from rostral to caudal.

Dental arcade and tooth band. (Fig. 3B) Rostrally dental arcade rounded. Outer row generally occupying almost total length of dentigerous arm of premaxilla, in two specimens (RMNH.PISC.83697 and RMNH.PISC.83621; Fig. 3B) edentulous part about 25% of arm. Outer row in lower jaw not, or just, reaching coronoid wing in most dissected specimens. In one case caudal-most tooth relatively high on coronoid wing. One or two inner rows in rostral part of both jaws, decreasing to zero in caudal part.

Teeth counts and setting. Outer row of upper jaw (l+r premaxilla) with 30–52 teeth. In both jaws outer-row teeth regularly set, their placement wider rostrally than laterally.

Tooth implantation. Outer-row teeth of premaxilla rostrally erect. Inner-row teeth recumbent. Outer-row teeth of lower jaw slightly procumbent, inner-row teeth erect.

Lower pharyngeal element. (Fig. 3 D,E) Lower pharyngeal element relatively small and slender (length/width ratio 1.2–1.3). Dentigerous area slightly broader than long (length/width ratio = 0.7–0.9). Suture straight.

Pharyngeal teeth counts. Caudal-most transverse row with about 30–38 teeth, medial longitudinal rows with eight to 11 teeth.

Pharyngeal teeth shape. Teeth in caudal-most transverse row hooked, major cusp only slightly incurved, blunt to slightly acute. Other teeth bevelled or pronounced. All teeth relatively fine and slender, medial teeth not coarser than other teeth.

Vertebrae. Total number of vertebrae in 57 specimens: 30 (12), 31 (39) or 32 (6), comprising 13–14 abdominal and 16–19 caudal vertebrae.

Live colouration males. (Fig. 4 A,B) Sexually active males with ivory to grey snout and cheek. Lips remarkably ivory-white with no or few pigment spots. Eye with grey outer ring and silver to golden inner ring. Lower jaw and interoperculum whitish. Gill cover silver, sometimes with grey to dusky flush. Dorsal head surface, dorsum and

flank silvery-grey, dorsum with bluish to purplish sheen, flank with yellow to greenish sheen. Chest, belly and ventral side silvery-white.

Pelvic fins black; in specimens of Emin Pasha Gulf, medial side sometimes red. Anal fin rostrally faintly to distinctly red, rest of fin hyaline. One to two dark yellow to orange egg dummies with hyaline ring present on caudal part of anal fin. Caudal fin orange-red to wine-red. Dorsal fin hyaline with red streaks and spots. Lappets hyaline or reddish, rostral lappets sometimes dusky.

Dark grey to blackish markings: Nostril-, interorbital-, and supraorbital stripes, sometimes rather distinct. Lachrymal stripe distinct, but relatively short (i.e. small blotch at caudal end of lachrymal generally not reaching caudal tip of maxilla), sometimes extending over iris. Irregular preopercular vertical bar generally present. Opercular blotch distinct. Three to five, generally faint vertical stripes on flank. Traces of dark-grey mid-lateral band occasionally present.

Live colouration females. Live females basically with same colours as males, lacking bluish-purplish and yellow-greenish sheens and distinct red colouration in fins, but sometimes with faint red flush in caudal fin. In females upper lip usually with more pigment than in males. Of markings on head, only lachrymal stripe and opercular blotch distinct. Mid-lateral band sometimes more distinct than in males, vertical stripes faint.

Preserved colouration of males and females. (Fig. 5) Body light brown, dorsally darker than ventrally. Snout, lips and lower jaw coloured as old ivory. Fins hyaline and light grey-brown in both sexes, except for black pelvic fins in adult males. Same markings, but slightly more distinct, as in live specimens.

Distribution. *Haplochromis argens* is only known from the Tanzanian part of Lake Victoria. Specimens were caught in the Mwanza Gulf (from entrance of Stuhlmann Sound to entrance of gulf in north), in the south-western part of the Speke Gulf (near its entrance), in the area around Kome Island, and in the Emin Pasha Gulf (Fig. 1).

Habitat. *Haplochromis argens* is a pelagic species from the littoral and sub-littoral zone. At night the species is virtually restricted to the two upper metres of the water column (Witte 1984b, Goldschmidt et al. 1990). By day, the highest densities were found at two to three metres from the surface, but individuals of this species were also caught with bottom trawls over sand and mud bottoms, and in gill nets and traps near rocks (Goldschmidt et al. 1990, Witte et al. 1992b).

Abundance. During 1979–1982, *H. argens* was present in 70% of the bottom-trawl tows by day and in 100% of the surface trawl tows at night; the mean numbers of individuals per tow ranged from 6.2 to 18.3, respectively (Table 2). In 1987–1988, it occurred in 3% of the bottom trawl tows and the mean number of individuals per tow was 0.03; the species was absent in surface trawls. Thirty-four bottom-trawl tows in 1990–1999 captured no *H. argens*. From 2001 to 2011 more than 150 bottom-trawl tows contained about 15 individuals of *H. argens*, corresponding to a decline in catch per unit effort of more than 50 times compared to the 1979–1982 captures; no individuals were caught with surface trawls.

Table 2. Frequencies of occurrence (Foo) in trawl tows and mean numbers (± SD) per tow of *Haplochromis argens*. Tows of 10 minutes duration were made with bottom trawls (day) at stations E to J (depth range 7–14 m) and with surface trawls (night) at station G (14 m deep); in the period 1990-1999 no surface trawls were made; n indicates number of trawl tows.

Station	Bottom trawl day	1979–1982† n = 104	1987–1988† n = 29	1990–1999‡ n = 34	2001–2011§ n > 150
E–J	Foo	70 %	3 %	0 %	< 10 %
	Mean nr	6.2 ± 12.2	0.03 ± 0.19	0	< 0.1
	Surface trawl night	**1981/1982 n = 8**	**1987-1988| n = 26**	-	**2001-2011§ n = 15**
G	Foo	100 %	0 %	-	27 %
	Mean nr	18.3 ± 12.4	0	-	0.5 ± 0.9

† Data from Witte et al. (1992b); ‡ data from Witte et al. (2000); §unpublished data from J.H Wanink; M.A. Kishe-Machumu, J.C. van Rijssel and F. Witte; | data from Wanink and Witte (1998).

Food. Before the ecological changes in Lake Victoria, the diet of *H. argens* comprised mainly zooplankton during the day; *Chaoborus* larvae were important at night (Goldschmidt et al. 1990). The current diet is unknown, but all the studied resurgent species in the Mwanza Gulf changed their diet (e.g. van Oijen and Witte 1996, Katunzi et al. 2003, Kishe-Machumu et al. 2008).

Breeding. *Haplochromis argens* is a female mouth brooder. Spawning sites are located at depths < 9 m (Goldschmidt and Witte 1990).

Etymology. In reference to the silver male colouration, *H. argens* was given the nickname "argens" under the false assumption it was Latinized Greek for silver. Since this species is well known under its cheironym, we think it is best to upgrade the nickname to the species' epithethon.

Comparisons. The zooplanktivorous species *H. (Yssichromis) laparogramma* Greenwood & Gee, 1969, *H. (Y.) pyrrhocephalus* Witte & Witte-Maas, 1987 and *H. (Y.) heusinkveldi*, Witte & Witte-Maas, 1987, have shorter bicuspid teeth in the oral jaws than *H. argens*, and generally the premaxillary dentigerous arm is edentulous over the caudal $^{1}/_{4}$ -$^{1}/_{3}$ versus the dentigerous portion extending almost to the caudal end of the dentigerous arm. The dental features of the zooplanktivorous/insectivorous *H. tanaos* van Oijen & Witte, 1996 and *H. thereuterion* van Oijen & Witte, 1996, are more or less similar to those of *H. argens*, but the former two species have more unicuspids. *Haplochromis argens* is further distinguished from these and other species by its colouration. Sexually active males of *H. tanaos* are dark blue, the females silvery with a distinct mid-lateral band and slightly less distinct dorso-lateral band. Sexually active males of *H. thereuterion* are black, the females coloured like females of *H. tanaos* (van Oijen and Witte 1996). The body of *H. argens* is less slender (BD 26.0–30.7% of SL, mean 28.2%, Table 1) than that of *H. tanaos* and *H. thereuterion* (22.1–27.1% and 24.4–27.6% of SL, respectively; Tables 3 and 7 in van Oijen and Witte 1996). Live *H. argens* is similar to (juvenile) *H. cassius* in colouration and general habitus. However, *H. cassius* has a broad, well defined mid-lateral band (Greenwood and Barel 1978), more and distinctly longer unicuspid teeth, more

Table 3. Measurements of *Haplochromis goldschmidti* sp. n., proportional to standard length or head length. Means and standard deviations were calculated over all measured type specimens, including the holotype.

		Holotype	Paratypes (n = 18) (n = 18)	Mean ± SD (n = 19) (n = 19)
SL (mm)		60.3	51.7–69.2	61.2 ± 4.6
BD	%SL	25.2	25.0–27.3	26.2 ± 0.7
PFL	%SL	27.4	24.2–29.3	27.4 ± 1.3
CPL	%SL	19.4	17.8–22.6	20.2 ± 1.1
CPD	%SL	9.0	8.5–10.4	9.6 ± 0.5
CFL	%SL	23.9	22.2–25.2	24.4 ± 0.8
HL	%SL	30.5	31.0–34.6	32.9 ± 0.9
SnL	%HL	26.6	23.7–29.7	26.4 ± 1.3
SnW	%HL	26.1	24.1–27.8	25.8 ± 1.2
HW	%HL	42.9	37.2–44.2	40.6 ± 1.7
IOW	%HL	21.7	19.3–21.7	20.7 ± 0.8
POW	%HL	26.1	22.1–27.3	24.1 ± 1.4
LaW	%HL	22.3	19.8–24.4	22.0 ± 1.3
POD	%HL	13.6	11.7–18.0	14.4 ± 1.8
EyL	%HL	35.9	32.7–40.2	36.5 ± 2.2
EyD	%HL	34.2	28.5–35.0	32.1 ± 1.8
ChD	%HL	14.1	13.1–16.3	15.0 ± 1.1
LJL	%HL	42.1	39.0–45.6	41.0 ± 1.6
LJW	%HL	12.5	11.7–18.0	14.0 ± 1.5
EyD/EyL		1.0	0.8–0.9	0.9 ± 0.0
LJL/LJW		3.4	2.2–3.6	3.0 ± 0.3

curved and more widely set teeth, and thicker lips than *H. argens*. The maximum size of *H. cassius* (99.0 mm SL) is larger than that of *H. argens*, but when comparing similar size ranges (see material and methods) *H. argens* has: a smaller head (ratio HL/SL: 31.0 – 35.6%, mean 32.9% versus 35.0 – 36.0%, mean 35.5% in *H. cassius*); a shorter snout (ratio SnL/HL: 23.6 – 29.7%, mean 26.6% versus 29.8 – 32.6%, mean 31.2% in *H. cassius*); larger eyes (ratio EyL/HL: 30.9 – 39.0%, mean 35.7% versus 26.8 – 28.8%, mean 28.3% in *H. cassius*). For comparison with *Haplochromis goldschmidti* sp. n., see below.

***Haplochromis goldschmidti* Witte, Westbroek & de Zeeuw, sp. n.**
urn:lsid:zoobank.org:act:06762084-8C0C-49CC-A48D-065244CF8457
http://species-id.net/wiki/Haplochromis_goldschmidti
Figs 6–9, Table 3

Cheironyms used. *Haplochromis* "dusky argens"; Goldschmidt 1989a: 148, 158, 160, 162, 166; Goldschmidt and de Visser 1990: 129, 130, 132; Goldschmidt 1991: 182, 187; van der Meer 1991b: 9–11, 15, 16, 19–22; van der Meer et al. 1995: 116, 117, 122–124, 126, 127.

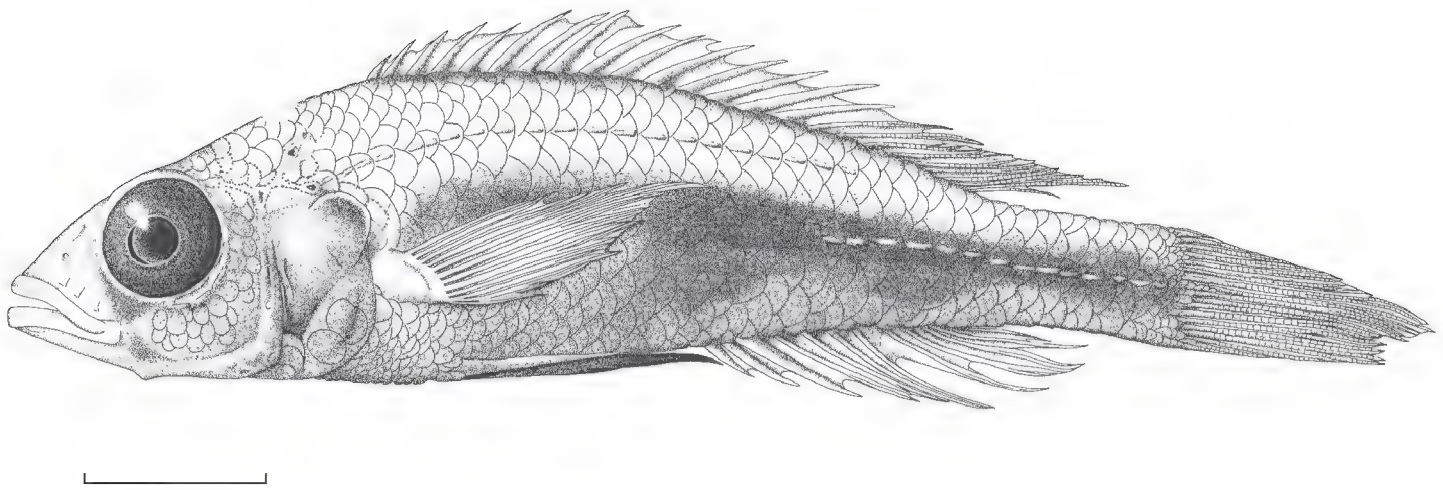

Figure 6. Habitus of *Haplochromis goldschmidti* sp. n. ♂ (holotype, RMNH.PISC.83573). Scale bar equals 10 mm. Drawing by I. Westbroek, missing (= dotted) scales added by M. van Oijen.

Type-locality. Tanzania, Lake Victoria, Emin Pasha Gulf (ca 2°35'–2°41'S; 31°47'–31°59'E).

Holotype. RMNH.PISC.83573[3], ♂, 60.3 mm SL, 23.vi.1985, HEST.

Paratypes. Collected by the *Haplochromis* Ecology Survey Team (HEST). Size of specimens given as standard length. RMNH.PISC.80480[4], ♂, 53.6 mm, 23.vi.1985; RMNH.PISC.80481, ♂, 56.8 mm, 23.vi.1985; RMNH.PISC.80482[4], ♂, 63.4 mm, 23.vi.1985; RMNH.PISC.80483[4], ♂, 52.9 mm, 23.vi.1985; RMNH.PISC.80484[4], ♂, 65.3 mm, 23.vi.1985; RMNH.PISC.80485[4], ♂, 69.2 mm, 23.vi.1985; RMNH.PISC.80493[4], ♂, 50.7 mm, 23.vi.1985; RMNH.PISC.80494[4], ♂, 52.2 mm, 23.vi.1985; RMNH.PISC.80495[5], ♂, 58.7 mm, 23.vi.1985; RMNH.PISC.80496[5], ♂, 57.4 mm, 23.vi.1985; RMNH.PISC.80497[5], ♂, 55.0 mm, 23.vi.1985; RMNH.PISC.80498[5], ♂, 60.4 mm, 23.vi.1985; RMNH.PISC.80499[5], ♂, 67.4 mm, 23.vi.1985; RMNH.PISC.80501[5], ♂, 61.1 mm, 23.vi.1985; RMNH.PISC.80502[5], ♂, 62.6 mm, 23.vi.1985; RMNH.PISC.80503[5], ♂, 57.7 mm, 23.vi.1985; RMNH.PISC.80507[5], ♂, 52.8 mm, 23.vi.1985; RMNH.PISC.80508[5], ♂, 62.9 mm, 23.vi.1985; RMNH.PISC.80512[5], ♂, 59.3 mm, 23.vi.1985; RMNH.PISC.80513[5], ♂, 63.6 mm, 23.vi.1985; RMNH.PISC.80514[5], ♂, 61.7 mm, 23.vi.1985; RMNH.PISC.83574[3], ♂, 62.6 mm, 23.vi.1985; RMNH.PISC.83575[4], ♂, 57.5 mm, 23.vi.1985; RMNH.PISC.83576, ♂, 58.2 mm, 23.vi.1985; RMNH.PISC.83577[3], ♂, 62.5 mm, 23.vi.1985; RMNH.PISC.83578[3], ♂, 69.2 mm, 23.vi.1985; RMNH.PISC.83579[3], ♂, 64.9 mm, 23.vi.1985; RMNH.PISC.83580[3], ♂, 62.9 mm, 23.vi.1985; RMNH.PISC.83581[3], ♂, 51.7 mm, 23.vi.1985; RMNH.PISC.83582[3], ♂, 52.4 mm, 23.vi.1985; RMNH.PISC.83583[3], ♂, 57.7 mm, 23.vi.1985; RMNH.PISC.83584[3], ♂, 55.4 mm, 23.vi.1985; RMNH.PISC.83585[3], ♂, 61.9 mm, 23.vi.1985; RMNH.PISC.83586[3], ♂, 65.4 mm, 23.vi.1985; RMNH.PISC.83664[3], ♂, 56.2 mm, 23.vi.1985; RMNH.PISC.83665[3], ♂, 63.2 mm, 23.vi.1985; RMNH.PISC.83666[3], ♂, 65.5 mm, 23.vi.1985; RMNH.PISC.83667[3], ♂, 60.7 mm, 23.vi.1985; RMNH.PISC.83668[3], ♂, 64.9 mm, 23.vi.1985; RMNH.PISC.83669[3], ♂, 65.8 mm, 23.vi.1985; RMNH.PISC.83670[3], ♂, 60.0 mm, 23.vi.1985; RMNH.PISC.83695[1, 2, 4], ♂, 56.2 mm, 23.vi.1985; RMNH.PISC.83696[1, 4], ♂, 58.0 mm, 23.vi.1985; RMNH.PISC.83699[1,

[5], ♂, 61.5 mm, 23.vi.1985; RMNH.PISC.83700[1, 5], ♂, 55.3 mm, 23.vi.1985; RMNH.PISC.83701[2, 5], ♂, 61.6 mm, 23.vi.1985; RMNH.PISC.83702[1, 2, 5], ♂, 61.1 mm, 23.vi.1985; AMNH 255036[5], ♂, 61.4 mm, 23.vi.1985; BMNH 2012.1.5.3[4], ♂, 61.6 mm, 22.vi.1985; NSMT-P 106960[4], ♂, 64.8 mm, 22.vi.1985.

[1] dissected to describe the oral jaws and contents of stomachs and intestines; [2] dissected to describe pharyngeal jaws and to count gill filaments; [3] proportional measurements taken; [4] colour picture available; [5] colour picture of anal fin available.

Diagnosis. Small sized (< 7 cm SL), slender (BD < 28% SL), micrognathic, zooplanktivorous *Hapolochromis* species (LJL < 45% HL in all but one specimens) with a slightly curved to straight dorsal head profile. Mainly bicuspid teeth in oral jaws. Generally premaxillary dentigerous arm edentulous over caudal $^{1}/_{5}$ - $^{1}/_{4}$. Males silvery with dusky flush on chest, flank, ventral side and ventral half of caudal peduncle.

Description. Proportional measurements of type material provided in Table 3.

Habitus. See Fig. 6. Body slender. Dorsal head profile straight to slightly curved. Premaxillary pedicel slightly prominent. Mouth oblique. Lips not thickened. Medial part of premaxilla slightly expanded to expanded. Caudal part of maxilla not bullate. Vertical through caudal tip of maxilla running through iris, just rostral to pupil. Lateral snout outline isognathous and obtuse, in large specimens sometimes slightly prognathous. Jaws equal anteriorly or lower jaw slightly protruding. Mental prominence slightly pronounced. Retro-articular processes of right and left mandible touching each other, interrupting ventral body outline. Eye approximately circular (occasionally slightly elongated) and medium to large in size. Distinct aphakic aperture present in pupil. Cephalic lateral line pores not enlarged.

Scales. Cheek, gill cover, and rostral part of the dorsal head surface with cycloid scales. Nape and rostral part of dorsum with a mixture of cycloid and weakly ctenoid scales. Chest mainly with ctenoid scales, occasionally weakly ctenoid or cycloid. Scales on remaining part of body mainly ctenoid. Scales on chest smaller than those on ventral and ventro-lateral part of body; size transition gradual. Small elongated scales on basal quarter to one third of caudal fin. Four to 5.5 (mode 5) scales between upper lateral line and dorsal-fin origin, four to seven (mode 6) between between pectoral- and pelvic-fin bases.

Fins. Pelvic fins just reaching or slightly surpassing rostral-most point of anal-fin origin. Pelvic fins with first soft rays slightly produced, occasionally filamentous. Caudal tip of anal fin not reaching caudal-fin origin. Caudal-fin outline truncate to slightly emarginate.

Gill apparatus. Description of gill apparatus based on lateral gill rakers and lateral hemibranch of first gill arch. Number of gill rakers on lower part of first gill arch 10–12 (one specimen with 13). Lower two to three rakers reduced (= very short), next one to two short, followed by two to seven slender and longer ones. Remaining rakers hooked, bifid, or trifid. Generally rakers closely set, viz. touching each other over major part of length. Number of gill filaments 87 to 93.

Viscera. Ratio between intestine length and SL: 1.0–1.2 (n = 5).

Oral jaws. (Fig. 7 A,B) Premaxillary ascending arm equal to or longer than dentigerous arm (asc./dent. arm ratio 1.0 to 1.1). Angle between arms 77° to 81°. Symphyseal articulation facet not present, lower jaw slightly more elongated than generalized

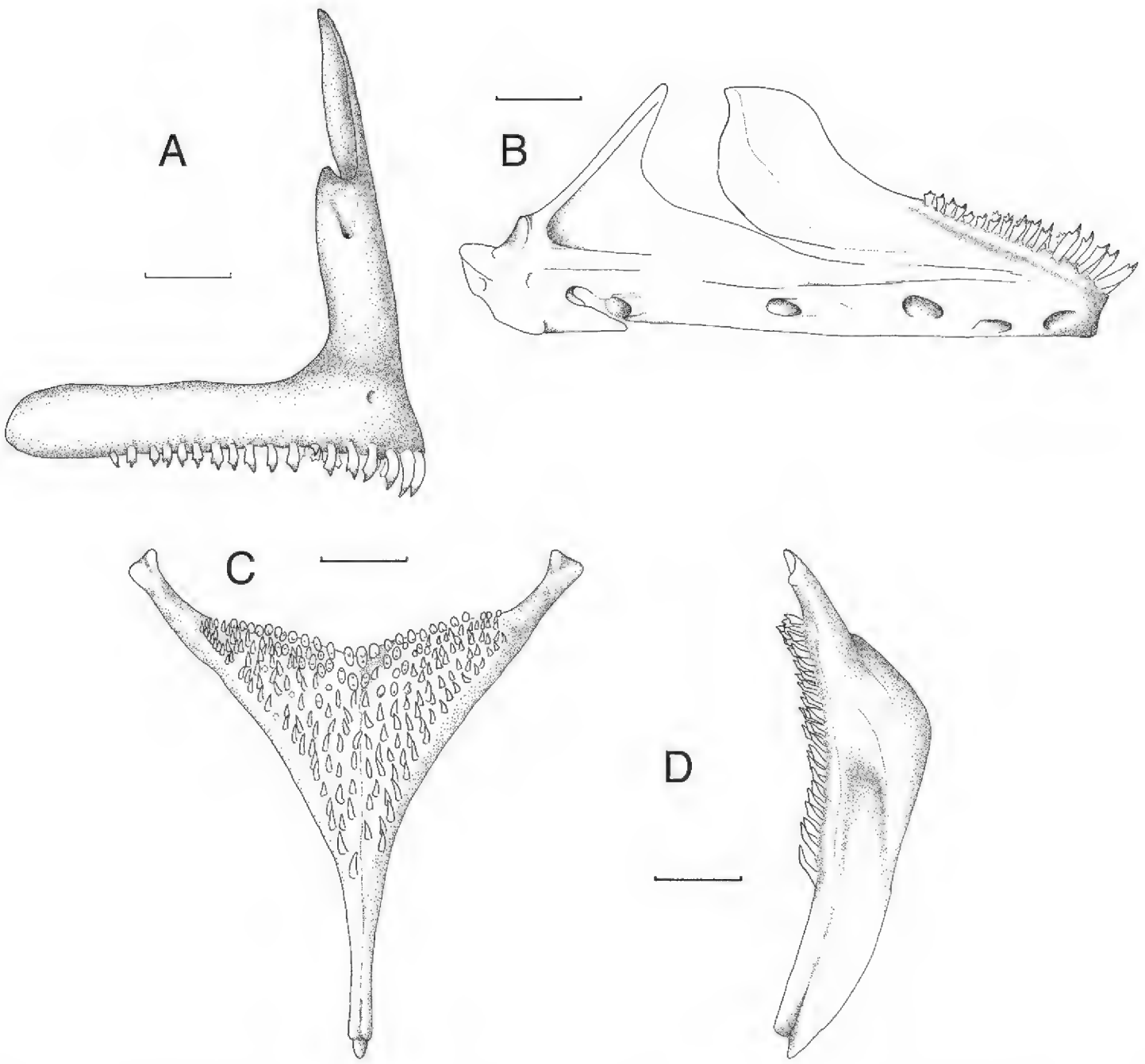

Figure 7. Skeletal elements of *Haplochromis goldschmidti* sp. n. **A** Right premaxilla, lateral view (RMNH.PISC.83695) **B** Right lower jaw, lateral view (RMNH.PISC.83695) **C** Lower pharyngeal element, dorsal view (RMNH.PISC.83701) **D** Lower pharyngeal element, lateral view (RMNH.PISC.83701). Scale bars equal 1 mm. Drawn by I. Westbroek.

type (length/height ratio 2.3 to 2.8). Upper half of dentary with distinct outwardly directed flare. Mental prominence slightly pronounced.

Oral teeth shape. (Fig. 7 A,B) Teeth of outer row in both jaws mainly bicuspid, with some unicuspid or tricuspid teeth interspersed. Major cusp of bicuspids isoscelene to subequilateral, protracted and acutely pointed. Flange occasionally present on major cusp. Minor cusp short compared to major cusp. Cusp gap rather narrow. In labial view neck moderately slender to normal, crown moderately expanded. In lateral view, crown compressed. Outer-row teeth in both premaxilla and lower jaw recurved. Inner rows in both jaws with mainly tricuspid or weakly tricuspid teeth.

Oral teeth size. Outer-row teeth relatively slender, gradually decreasing in size from rostral to caudal.

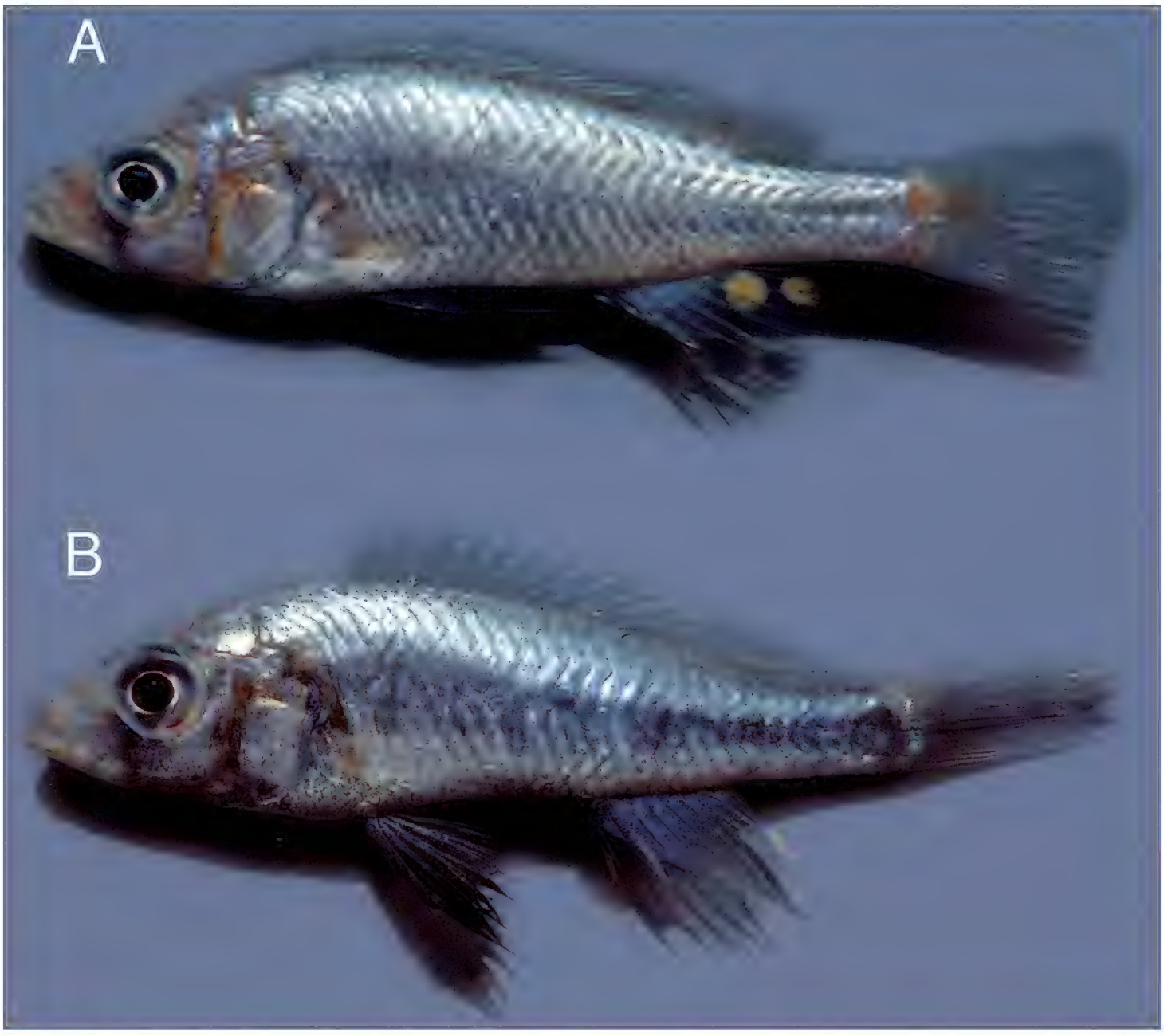

Figure 8. Live colours of *Haplochromis goldschmidti* sp. n. **A** sexually active ♂, 53.6 mm SL (paratype, RMNH.PISC.80480) **B** sexually active ♂, 57.5 mm SL (paratype, RMNH.PISC.83575).

Dental arcade and tooth band. Rostrally dental arcade rounded. Outer row occupying $^{3}/_{4}$ to $^{4}/_{5}$ of premaxillary dentigerous arm. One to two inner rows in both jaws.

Teeth counts and setting. Outer row of upper jaw (l+r premaxilla) with 33–47 teeth. In both jaws outer-row teeth regularly set. Teeth set wider rostrally than laterally.

Tooth implantation. Outer-row teeth of premaxilla rostrally erect. Inner-row teeth recumbent. Outer-row teeth of lower jaw slightly procumbent, inner-row teeth erect.

Lower pharyngeal element. (Fig. 7 C,D) Lower pharyngeal element relatively small and slender (length/width ratio 1.2–1.3). Dentigerous area slightly broader than long (length/width ratio 0.7–0.9). Suture straight.

Pharyngeal teeth counts. Caudal-most transverse row with 25–34 teeth, medial longitudinal rows with nine to 10 teeth.

Pharyngeal teeth shape. Teeth in caudal-most transverse row hooked, major cusp only slightly incurved, blunt to slightly acute. Other teeth bevelled or pronounced. All teeth relatively fine and slender, medial teeth not coarser than other teeth.

Figure 9. Preserved colours of *Haplochromis goldschmidti* sp. n. ♂ 60.3 mm SL (holotype, RMNH. PISC.83573). Scale bar equals 10 mm.

Vertebrae. Total number of vertebrae in 19 specimens: 30 (2), 31 (16) or 32 (1), comprising 13–14 abdominal and 16–18 caudal vertebrae.

Live colouration males. (Fig. 8 A,B) Sexually active males with grey-white snout, cheek and gill cover. Lips grey-white, generally with distinct black pigment spots. Eye with grey outer ring and silver inner ring. Dorsal head surface and dorsum silvery-grey. Chest, ventral side, flank and ventral part of caudal peduncle silvery-grey with dusky flush. Flush most distinct on flank and caudal peduncle and occasionally absent on ventral side, sometimes extending over suboperculum, interoperculum, branchiostegal membrane and lower jaw.

Pelvic fins black. Anal fin rostrally hyaline-grey with bluish sheen, remaining part hyaline. One to two pale-yellow to yellow egg dummies surrounded by hyaline ring on caudal part of anal fin. Caudal fin hyaline with bluish sheen; dusky flush on caudal peduncle may extend over rostral part of caudal fin. Dorsal fin hyaline with bluish sheen and faint dusky lappets.

Dark grey to blackish markings: Faint nostril-, interorbital- and supraorbital stripes sometimes present. Lachrymal stripe occasionally slightly longer than in *H. argens*, but often less distinct. Preopercular vertical stripe generally not clear. Opercular blotch present.

Preserved colouration of males. (Fig. 9) Body light brown. Chest, ventral side, flank and ventral part of caudal peduncle dusky to dark brown. Dark brown colour on caudal peduncle sometimes giving impression of broad mid-lateral band. Fins transparent to light grey-brown except for pelvics, which are black in adult males. Same markings present as in live specimens.

Distribution. *Haplochromis goldschmidti* is only known from the southern part of the Emin Pasha Gulf of Lake Victoria (Fig. 1).

Habitat. *Haplochromis goldschmidti* was caught over mud bottoms at depths of 4–10 m.

Food. Stomach and intestines of five examined specimens caught by day contained mainly zooplankton (mainly copepods, but also some cladocerans) and some insects (*Chaoborus* larvae and pupae).

Breeding. Based on the egg dummies on the anal fin of males, *H. goldschmidti* is probably a female mouth brooder.

Etymology. This species is named in honour of Dr Tijs Goldschmidt in appreciation for his work on haplochromine cichlids of Lake Victoria. As a member of the *Haplochromis* Ecology Survey Team, Tijs Goldschmidt worked in Tanzania (1981–1986) on the ecology and evolution of zooplanktivorous and detritivorous cichlids. *Haplochromis goldschmidti* is one of the species on which he based his theory on the possible role of egg-dummy divergence in speciation of haplochromines (Goldschmidt and de Visser 1990). With "Darwin's Dreampond" (Goldschmidt 1996) - originally published as "Darwins Hofvijver" (Godschmidt 1994) and translated in eight languages - Tijs Goldschmidt started his career as a writer and brought the human-induced extinction of the Lake Victoria cichlids to the attention of a worldwide public. The specific epithet, *goldschmidti*, is a Latinized version (genitive case) of the surname.

Comparisons. Sexually active males of *H. goldschmidti* and *H. argens* are very similar, but distinguishable by live colouration. *Haplochromis goldschmidti* has a dusky flush on its flank and *H. argens* a yellow to greenish sheen. In contrast to *H. argens*, red is generally absent on the fins of *H. goldschmidti*, only occasionally very faint traces of red are present on the caudal and dorsal fins. *Haplochromis goldschmidti* has plain yellow egg spots, while the egg spots of *H. argens* are orange yellow (Goldschmidt and de Visser 1990). Generally, *H. goldschmidti* has more pigment spots on its lips than *H. argens*. The body depth in *H. goldschmidti* is less deep than in *H. argens*. The snout width, lachrymal width and lower jaw width are generally larger in *H. goldschmidti* (Tables 1, 3, 4).

Sexually active males of *H. goldschmidti* are distinguished from *H. tanaos* and *H. thereuterion*, two other slender zooplanktivores, by colouration. A distinct mid- and dorsal-lateral band is absent in males of *H. goldschmidti*, whereas they are present in *H. tanaos* and *H. thereuterion* (sometimes difficult to distinguish in the latter). A nape band is lacking in *H. goldschmidti*, but present in *H. tanaos*.

Comparison of species and populations

The MANCOVA of the linear measurements of males of *H. goldschmidti* and both populations of *H. argens* shows that SL is a significant covariate ($P < 0.001$), explaining the largest part of the variance ($F = 81.406$). The two species differ significantly (species effect, $P < 0.001$), and the same holds for the populations from the Mwanza Gulf and the Emin Pasha Gulf (location effect, $P = 0.007$), with the effect of species explaining more of the variance ($F = 9.262$) than the effect of location ($F = 2.494$). There is also a significant interaction between SL and location, however it does not explain much of the variance ($F = 2.545$).

From the ANCOVAs of the individual measurements, the adjusted means and their differences were calculated (Table 4).

There is a significant species effect in eight (BD, CPL, CFL, SnW, POW, LaW, POD and LJW) of the 18 measurements, and in three of these measurements (CPL, POW, POD) this is the only significant effect. The other measurements (BD, CFL, SnW, LaW and LJW) also differ significantly between the two populations of *H. argens* (= effect of location). In addition, for BD, a significant interaction ($P = 0.031$) between the effects of location

Table 4. Adjusted means (rounded to the nearest 0.1 mm), their differences (in %) and significance levels of the ANCOVAs of linear measurements. Both populations of *Haplochromis argens* are compared to *H. goldschmidti*. The mean values represent antilogged adjusted means calculated from the ANCOVA analyses (sample mean adjusted for a common mean standard length and a common regression line for the three groups). Adjusted means and differences are not applicable (NA) when the slopes of the relationships differ (i.e., in case of a significant interaction between location and SL). Estimated differences were calculated from adjusted means. Parameter estimates were derived from the GLM (analysis of covariance) procedure. Significance levels (*P*) of the effect of species (Spec.), location (Loc.) and the interaction between SL and location (Loc. * SL) are given when below 0.05.

	H. argens	*H. argens*	*H. goldsch*	*H. argens*	*H. argens*	Spec.	Loc.	Loc. * SL
	Mwanza	Emin P	Emin P	Mwanza	Emin P			
	Mean	Mean	Mean	% diff.	% diff.	P	P	P
BD	NA	NA	NA	NA	NA	< 0.001	0.041	0.031
PFL	17.6	16.9	16.9	4.1	0.0	ns	< 0.001	ns
CPL	12.9	12.9	12.4	3.3	3.3	0.012	ns	ns
CPD	6.3	6.0	6.0	5.5	0.0	ns	< 0.001	ns
CFL	15.0	14.6	15.1	-0.6	-3.2	0.007	0.016	ns
HL	20.4	20.4	20.4	0.0	0.0	ns	ns	ns
SnL	5.4	5.4	5.4	0.0	0.0	ns	ns	ns
SnW	5.1	4.8	5.3	-2.7	-9.0	< 0.001	< 0.001	ns
HW	NA	NA	NA	NA	NA	ns	< 0.001	< 0.001
IOW	4.3	4.2	4.2	2.7	0.0	ns	0.011	ns
POW	4.7	4.7	4.9	-3.5	-3.5	0.004	ns	ns
LaW	4.2	4.0	4.5	-7.3	-10.4	< 0.001	0.046	ns
POD	3.1	3.1	2.9	5.4	5.4	0.030	ns	ns
EyL	NA	NA	NA	NA	NA	ns	< 0.001	< 0.001
EyD	6.5	6.5	6.5	0.0	0.0	ns	ns	ns
ChD	3.5	3.1	3.1	11.7	0.0	ns	< 0.001	ns
LJL	NA	NA	NA	NA	NA	ns	0.039	0.040
LJW	2.8	2.6	2.8	-2.1	-9.1	0.001	0.003	ns

and SL indicate an increasing relative difference in BD (with increasing standard length) between the estimations for the populations from the different locations (Table 4, Fig. 10).

In the measurements, except for BD, in which there is a significant effect of species and location, the population of *H. argens* from the Emin Pasha Gulf differs more from *H. goldschmidti* than does the population of *H. argens* from the Mwanza Gulf. Especially in width measurements from the oral and suspensorial compartment, SnW, LaW and LJW, this is apparent (Fig. 10). In BD, *H. argens* from the Mwanza Gulf differs more from *H. goldschmidti* than does *H. argens* from the Emin Pasha Gulf (Fig. 10).

The effect of location is significant in 12 of the 18 measurements, and for PFL, CPD, IOW and ChD, this is the only significant effect; these measurements are significantly larger in *H. argens* from the Mwanza Gulf than in *H. argens* from the Emin Pasha Gulf and *H. goldschmidti*. In four measurements in which there is a significant effect of location, the two-way interaction is significant as well. For BD, HW and LJL, the relative difference between *H. argens* from the Mwanza Gulf and both *H. argens*

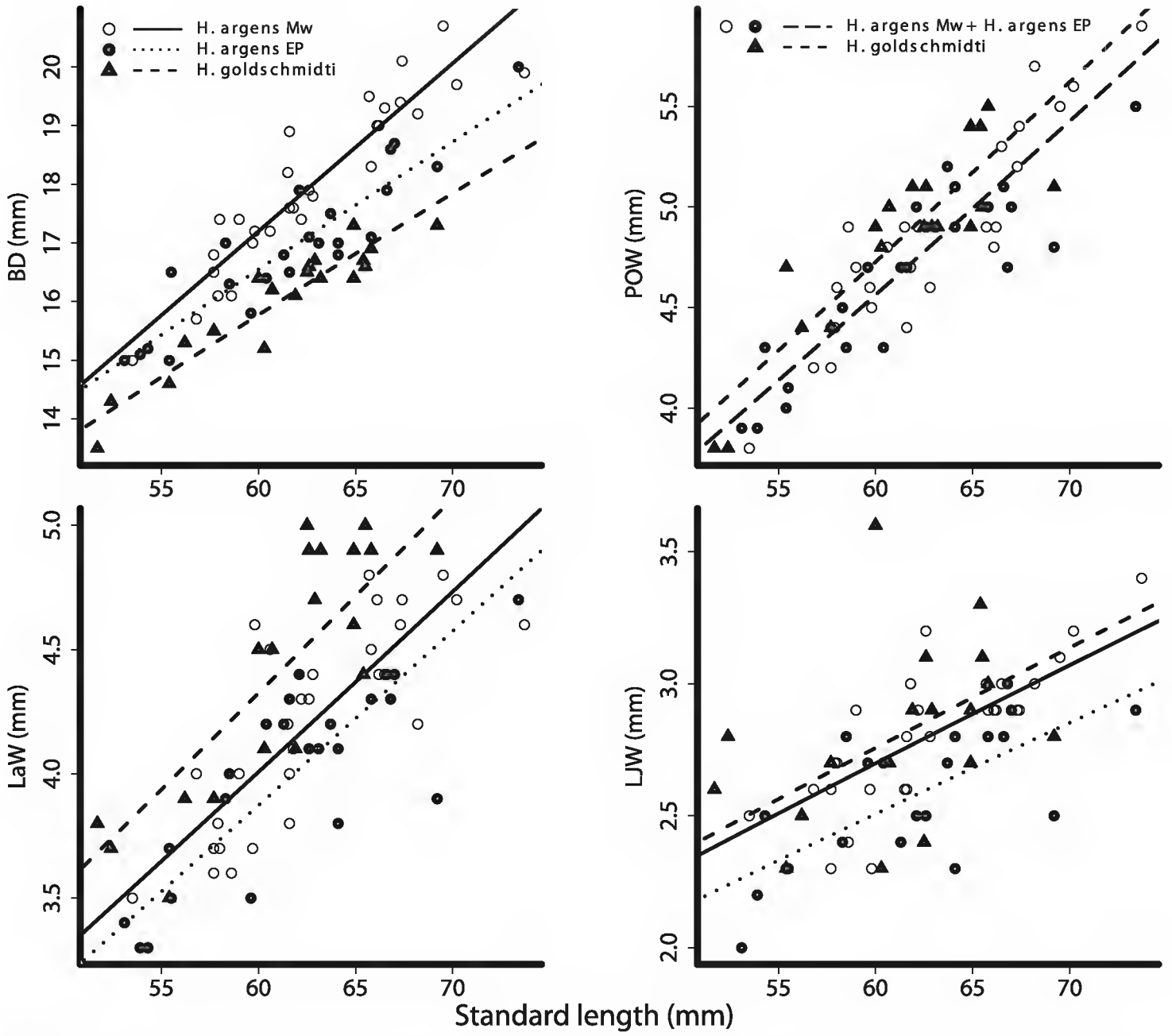

Figure 10. Plots of taxonomic measurements as a function of standard length. Body depth (BD), preorbital width (POW), lower jaw width (LJW) and lachrymal width (LaW). Open circles - *Haplochromis argens* from the Mwanza Gulf (Mw); closed circles - *H. argens* from the Emin Pasha Gulf (EP); triangles - *H. goldschmidti*. Power curves determined from GLM parameter estimates, solid line - *H. argens* from the Mwanza Gulf; dotted line - *H. argens* from the Emin Pasha Gulf; dashed line - *H. goldschmidti*, long dashed line (POW) - *H. argens* from both locations (MW + EP).

and *H. goldschmidti* from the Emin Pasha Gulf increases with SL. For EyL, however, the relative difference between *H. argens* from the Mwanza Gulf and both *H. argens* and *H. goldschmidti* from the Emin Pasha Gulf decreases with SL.

Discussion

Females of *H. goldschmidti*

In this paper, females of *H. goldschmidti* have not been described since it was difficult to distinguish the females from females of *H. argens* in the field. Samples of females,

which presumably contained both *H. argens* and *H. goldschmidti,* were collected during ecological surveys in the Emin Pasha Gulf, but unfortunately these samples were mislaid or may have been lost during the many moves of the material since its collection.

Specific status of *H. goldschmidti*

Since the field research of Greenwood (many papers bundled in 1981), male colouration has become a major character in species distinction of Lake Victoria cichlids. Indeed, experimental research has shown that male colouration plays a major role in female mate choice of Lake Victoria haplochromines (Seehausen and van Alphen 1998). However, Seehausen et al. (1998, 1999) also found some rock-dwelling species with a distinct polymorphism in breeding colours of sympatrically (and allopatrically) occurring males. These males did not differ in morphological characters, and mating experiments in tanks confirmed these colour polymorphisms (Seehausen and Bouton 1996; Seehausen et al. 1999). Nevertheless, we consider it unlikely that *H. argens* and *H. goldschmidti* represent an example of a species with male colour polymorphism, as apart from male body colouration there are at least four other presumably independent characters that differ in the two species (viz.: colour, position and number of egg spots (Goldschmidt and de Visser 1990); width measures of the head; body depth; differences in tooth shape). Based on the genotypic cluster species concept of Mallet (1995) it has been suggested that groups of haplochromine cichlids that differ in male nuptial colouration and one or more other characters that are likely to be genetically independent (e.g. dentition, body shape etc.) will be considered as different species (Seehausen et al. 1998). As will be clear from the comparison above, *H. argens* and *H. goldschmidti* fulfil these criteria.

Generic classification

Greenwood (1979, 1980) revised the Lake Victoria haplochromines and split them into more than 20 genera and subgenera. During the past decades there have been extensive debates on the validity of the genera defined by Greenwood (Hoogerhoud 1984; Meyer et al. 1990; Lippitsch 1993; Snoeks 1994; Seehausen 1996; van Oijen 1996; Seehausen et al. 1998). Because of the disagreements, and as a considerable number of the haplochromine species from Lake Victoria cannot be assigned to the "new" genera, we prefer to keep newly described species in the genus *Haplochromis* and add the generic names from Greenwood's revision of the Lake Victoria haplochromines (Greenwood 1979, 1980) between brackets in cases where the assignment is unequivocal.

In some studies *H. argens* has been assigned to *Yssichromis* (e.g. van Staaden et al. 1995; Chapman et al. 1995; Huber et al. 1997; Rosenberger and Chapman 2000; Melnychuk and Chapman 2002). However, even when adopting Greenwood's revision, for the following reasons we doubt whether this allocation to *Yssichromis* is correct.

According to Greenwood (1980: 24) "*Yssichromis* is an isolated lineage, defined by its autapomorphic features (shallow elongate body, and posteriorly edentulous premaxilla)". Though *H. argens* has a shallow, elongate body, it generally lacks a posteriorly edentulous premaxilla. Moreover, compared to the zooplanktivorous species assigned to *Yssichromis*, *H. argens* has a more piscivorous facies with some features that resemble those of *Prognathochromis*, e.g. a slightly prognathous lower jaw, a slightly pronounced mental prominence, the medial part of the premaxilla slightly expanded. Further, its oral teeth are longer and have a more protracted and acute major cusp than the teeth of the zooplanktivores that were assigned to *Yssichromis*. Greenwood (1980: 23) wrote concerning *Yssichromis*: "Superficially, members of this genus resemble the *Prognathochromis* lineage, especially members of the subgenus *Tridontochromis*. However, *Yssichromis* species retain several generalized features in the syncranium, and the lower jaw length is shorter, although some overlap does occur." The lower jaw of *H. argens* is indeed too short for the species to be recognized as *Prognathochromis* (viz. 37.6–44.3% of HL, mean 40.5% versus 41–62%, modal range 45–53%), and judging from the radiographs, the neurocranium is of the generalized type. Based on the information above, the position of *H. argens* seems to be between *Yssichromis* and *Prognathochromis.*

Haplochromis goldschmidti has the two autapomorphic characters of *Yssichromis* and can thus be referred to as *H. (Y.) goldschmidti*. However, in some characters it seems to bridge the gap between *H. argens* and the species of the *Yssichromis* group, as its teeth are longer than those of the latter, but shorter than those of *H. argens*, and it has the medial part of the premaxilla slightly expanded to expanded. Both *H. argens* and *H. goldschmidti* lack the typical arrangement of the inner rows in the lower jaw described for *H. (Y.) laparogramma*, *H. (Y.) pyrrhocephalus* and *H. (Y.) heusinkveldi* by Witte and Witte-Maas (1987). These species have a single inner row except for the rostro-lateral corner, where two inner rows are present.

Considering the resemblance between *H. argens* and *H. cassius*, the latter assigned to the genus *Psammochromis* by Greenwood (1980), we investigated whether *H. argens* could be assigned to this genus. The main apomorpic character for *Psammochromis*, a dentary with each ramus inflated anteriorly and antero-laterally (Greenwood 1980), has not been found in *H. argens* (and also not in *H. goldschmidti*). Other diagnostic characters for the genus, like thickened lips and a maximum adult size of 100–123 mm SL, have been found in neither *H. argens* nor in *H. goldschmidti*. So there are no arguments for assigning the species to *Psammochromis*.

Comparison of *H. goldschmidti* with the populations of *H. argens*

In some morphological characters (e.g. body depth), *Haplochromis goldschmidti* is more similar to the sympatric population of *H. argens* than to the allopatric population of the latter in the Mwanza Gulf, whereas for other characters (snout width, lower jaw width) the opposite is true. It has been found in earlier studies that local adaptations related to environmental conditions may cause similar morphological shifts in several

species of Lake Victoria haplochromines (Bouton et al. 1999, 2002). A recent study by van Rijssel and Witte (2012) revealed a decrease in body depth of two resurgent zooplanktivorous species in the Mwanza Gulf in the 1990s, which they associated with increased predation pressure by Nile perch in that period. Local environmental conditions may result in morphological similarity between sympatric populations of different species. On the other hand, competition for food might provide a tentative explanation for the greater difference in width of the snout area between *H. goldschmidti* and the sympatric population of *H. argens* in the Emin Pasha Gulf. However, to confirm this, information would be needed about their feeding habits in the areas where the two species coexist and where *H. argens* occurs alone.

Endangered species

Eight zooplanktivorous haplochromine species that were common on our research transect in the Mwanza Gulf (Goldschmidt et al. 1990) had virtually disappeared by 1987 (Witte et al. 1992b). However, since the early 1990s a gradual recovery has been observed for three of these species: *H. pyrrhocephalus*, *H. laparogramma* and *H. tanaos* (Seehausen et al. 1997b, Witte et al. 2000). Since 2005, these species are even more common than they used to be in the 1970s (Witte et al. 2007a, 2012a, Kishe-Machumu 2012). In contrast, the other five species, including *H. argens*, remain rare or are absent. In 2002, *H. argens* was observed for the first time since its disappearance in 1987, and since then it has been caught only occasionally in the Mwanza Gulf (Table 2) and in the Speke Gulf (Mizoiri et al. 2008) in spite of intensive sampling programmes. The catch per unit effort on the research transect has declined more than 50 times, and it is likely that the species is in danger of extinction. We are not sure of the conservation status of *H. goldschmidti*, as we did not sample the Emin Pasha Gulf, the only area from which the species is known, after 1986. This restricted distribution makes the species vulnerable in any case.

In the successfully recovering zooplanktivorous haplochromine species, morphological changes were observed, which may have been caused by adaptive responses to the environmental changes, both through natural selection and phenotypic plasticity (Wanink and Witte 2000, Witte et al. 2008, Chapman et al. 2008, van der Meer et al. 2012; van Rijssel and Witte 2012). In some cases (introgression through) hybridization may have also taken place among zooplanktivores (Mzighani et al. 2010). Van Rijssel and Witte (2012) found that several successfully resurgent haplochromine species had a smaller head-surface area/caudal-peduncle area than in the past, which aids in predator escape because it facilitates burst swimming (Langerhans 2010). In the not or poorly recovering zooplanktivorous species *H. heusinkveldi*, and *H. piceatus* Greenwood & Gee, 1969, the head-surface area/caudal-peduncle area changed in the opposite direction (van Rijssel and Witte 2012). A preliminary study of the few individuals that were collected in the Mwanza Gulf in the 2000s suggests that this also was the case in *H. argens*. These changes in the ratio between head surface

and caudal peduncle will be further studied when more material becomes available in the future. Obviously, the recovering zooplanktivores are of great interest for future research, and the species descriptions in this paper contribute to the taxonomic baseline for these studies.

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